

Heart and aorta morphology of the deep-diving hooded seal (*Cystophora cristata*)

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Abstract: An investigation of the heart morphology of 8 male and 15 female hooded seals (*Cystophora cristata*) revealed that the heart is proportionately large and the aortic bulb is larger than that reported for most seals. Hooded seals of all ages have large hearts (0.64% of the body mass) and the right ventricle is proportionately longer and more muscular than reported for other seals. The bulb of the ascending aorta shows the large-diameter characteristic of seals capable of making long deep dives, and is constricted to a diameter of less than one-third in the descending aorta. In addition, the ascending aorta has a much greater concentration of elastin fibers than does the descending aorta. In combination with the large right ventricle, these features probably serve to increase lung perfusion during the hooded seal's surface recovery, and to maintain a high blood pressure throughout the cardiac cycle during diving bradycardia. That there was no substantive difference in the heart morphology of pups, yearlings, and adults, suggests that these features are important in the development of diving behavior, and agrees with the rapid behavioral and physiological development of hooded seal neonates.

Résumé : L'étude de la morphologie du coeur de 8 mâles et de 15 femelles du phoque à capuchon (*Cystophora cristata*) a révélé que le coeur est gros proportionnellement au reste du corps et que le bulbe aortique est plus gros que celui qui est signalé chez la plupart des phoques. Les phoques à capuchon de tous âges ont un gros coeur (0,64 % de leur masse totale) et leur ventricule droit est proportionnellement plus long et plus musculaire que celui des autres phoques. Le bulbe de l'aorte ascendante a un grand diamètre, un caractère typique des phoques qui font des plongées profondes de longue durée, et il comporte une constriction dont le diamètre est moins du tiers de la valeur la plus grande dans l'aorte descendante. De plus, l'aorte ascendante a une concentration d'élastine beaucoup plus grande que celle que l'on trouve dans l'aorte descendante. Combinées au ventricule droit, qui est de grande taille, ces structures contribuent probablement à augmenter la perfusion du poumon du phoque à capuchon à son retour en surface et à maintenir élevée sa tension artérielle pendant tout le cycle cardiaque lors d'une bradycardie de plongée. L'absence de différences importantes entre la morphologie du coeur des jeunes phoques et celle des phoques de 1 an ou des adultes indique que ces caractères sont importants pour le développement du comportement de plongée et elle est compatible avec la rapidité du développement comportemental et physiologique des phoques à capuchon nouveau-nés.

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Introduction

Since the early laboratory work of Irving et al. (1935) and Scholander (1940), the cardiorespiratory adaptations that seals have shown during forced dives have been of interest to researchers. However, the more recent development and implementation of heart-rate transmitters, time–depth recorders (TDRs), and other data-storage devices have enabled researchers to extensively document the diving capabilities of a wide variety of pinnipeds diving in natural conditions (Butler and Jones 1997). An awareness of the great depths, long submergences, and repeated dives (accompanied by short recovery times) by seals diving voluntarily has renewed researchers' interest in the role cardiac structures might play in the seal's dive response. As a result, there have been a series of studies

of the heart morphology of a number of pinnipeds with interpretations of adaptations to diving (Bryden and Lim 1969; Bryden 1971; Drabek 1975, 1977; King 1977; Bisailon 1982; van Nie 1985; Stewardson et al. 1999). In general, researchers have found that pinniped hearts are flat and broad with both ventricles forming the apex with a slight bifurcation. The typical mammalian arrangement of four chambers separated by tricuspid (right) and bicuspid (left) atrioventricular valves is seen. Tricuspid semilunar valves are at the bases of the pulmonary artery and ascending aorta. The common pattern of arterial branching from the arch of the aorta in pinnipeds is brachiocephalic, left common carotid, and left subclavian.

In addition to modifications in basic heart form, the elastic and bulbous ascending aorta of pinnipeds has received attention. While Burow (1838) indicated that the early anatomists were aware of this pinniped feature, and Murie (1874) made passing note of the bulbous aorta in the sea lion, it was not until Drabek (1975) conducted studies on several Antarctic phocids that it was first described in detail. Since then, the distensibility of the aortic bulb and its elastic recoil have been hypothesized to play a role in maintaining arterial pressure during the long diastolic intervals of diving bradycardia (Campbell et al. 1981; Rhode et al. 1986; Shadwick and

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Table 1. *Cystophora cristata* specimens used for heart measurements.

Seal				Heart measurement		
ID No.	Age	Sex	Mass (kg)	Mass (g)	Circumference (mm)	Height (mm)
1999.8104	<4 d	M	30.0	180	—	—
1999.8105	<4 d	M	31.0	228	—	—
Mean			30.5	204		
1999.8110	4–10 d	M	30.0	212	—	—
1999.8112	4–10 d	F	30.0	216	—	—
1999.8129	4–10 d	F	29.5	228	—	—
1999.8108	4–10 d	M	38.0	218	—	—
1999.8123	4–10 d	M	31.1	156	—	—
1999.8117	4–10 d	F	28.8	156	—	—
2000.1	4–10 d	M	48.0	288	255	73
2000.2	4–10 d	M	39.5	178	216	64
2000.5	4–10 d	F	50.0	238	262	70
2000.8	4–10 d	F	35.5	188	232	62
Mean ± SE			36.04±2.46	207.8±12.7	241±11	67.3±2.6
2000.11	1 year	M	53.0	394	299	87
2000.10	1 year	F	54.0	397	299	88
2000.12	1 year	F	50.0	326	280	89
Mean ± SE			52.3±1.2	327±23	293±6	88.0±0.6
1999.8101	Adult	F	176.5	1110	—	—
1999.8103	Adult	F	147.5	1004	—	—
1999.8106	Adult	F	142.5	942	—	—
1999.8107	Adult	F	152.5	972	—	—
1999.8109	Adult	F	160.5	1098	—	—
1999.8111	Adult	F	154.5	1102	—	—
2000.6	Adult	F	143.0	908	435	134
2000.7	Adult	F	179.0	1116	445	165
Mean ± SE			157.0±5.0	1031±30	440±5	150±16

Gosline 1995), as well as reducing cardiac work, and thus, conserving oxygen during dives (Blix and Folkow 1983).

Recently, Folkow and Blix (1995, 1999) reported that the diving behavior of hooded seals included the ability to dive to depths greater than 1000 m and to remain submerged longer than 52 min. This diving behavior is particularly impressive in light of the small body mass (98–235 kg) of the seals they studied. In fact, the only pinnipeds to dive deeper (1529 m) and longer (120 min) than hooded seals are the much larger male northern (*Mirounga angustirostris*, 2000 kg) and female southern (*Mirounga leonina*, 600 kg) elephant seals (Schreer and Kovacs 1997).

Although the cardiovascular anatomical adaptations that play a role in the deep- and long-diving behavior of pinnipeds have been described for some species (Drabek 1975; Rhode et al. 1986), the anatomy of the hooded seal's heart and aorta is unknown. Similarly, there is nothing known about the ontogeny of heart morphology or the role that it might play in the development of the cardiovascular control necessary for diving in juveniles. In light of the remarkable diving behavior of adults and the extremely short developmental period of pups (Bowen et al. 1985), the objective of this study was to characterize the hooded seal heart and aorta morphology and to compare it with that of other seal species.

Materials and methods

The hearts of 8 males and 15 females representing weaned pups, yearlings, and adults were studied (Table 1). Hearts

were taken in March and April of 1999 and 2000 in the pack ice off the Greenland coast (between 70° and 72°N and 12° and 18°W) under permit from the Norwegian National Committee on Ethics in Animal Experimentation and imported under the Marine Mammal Protection Act permit No. 782-1399. All animals were autopsied immediately following collection, and the hearts were either measured at the time of collection or stored cold and measured within 72 h. The hearts of the three yearlings were weighed when fresh, frozen, and then thawed, fixed in 10% formalin, and stored in 30% isopropyl alcohol until measurements were taken 2 months later. All hearts were treated in the same way, to avoid any measurement variability due to preservation protocol.

Measurements

Hearts were rinsed, flushed in water, and the pericardium and greater vessels removed before weighing on an electronic balance to the nearest gram. Measurements were taken with Helios needle calipers. Heart circumference was measured at the point of greatest circumference, and nonseptal ventricle walls were measured at their points of maximal thickness. Heart height was measured from the orifice of the pulmonary valve to the apex. The internal measurements of the right ventricle that were used to derive the ventricular length and width indices followed the rectilinear triangle used by Drabek (1975). Comparisons of mass-specific heart masses and relative heart sizes among age groups were performed

Table 2. Heart parameters of seals.

Species	N	Heart (mean \pm SE% TBM)	Heart form (mean \pm SE)	Right ventricle				Percent heart mass	Source
				Length index	Width index	Percent left ventricle thickness	Percent heart mass		
<i>Cystophora cristata</i>									
Newborns	2	0.66 \pm 0.08							This study
Weaned pups	10	0.59 \pm 0.03	28 \pm 0.7	93	59	84	22		This study
Yearlings	3	0.71 \pm 0.03	30 \pm 0.8	80	39	68	19		This study
Adults	8	0.68 \pm 0.01	34 \pm 3.1	102	46	58	22		This study
<i>Pagophilus groenlandicus</i>									
Pups	4	0.61 \pm 0.02							J.M. Burns, unpublished data
Adults	3	0.69 \pm 0.04							J.M. Burns, unpublished data
	6	0.59	33	69	55	33			Bisaillon 1982
<i>Mirounga leonina</i>									
Adults	37	0.7							Bryden 1971
<i>Leptonychotes weddellii</i>									
Adults	6	0.5 \pm 0.08	29	77	40	19	18		Drabek 1975
<i>Lobodon carcinophagus</i>									
Adults	3	0.5 \pm 0.04	37	70	50	29	19		Drabek 1975
<i>Ommatophoca rossii</i>									
Adults	2	0.5	36	62	42	35	18		Drabek 1975
<i>Hydrurga leptonyx</i>									
Adult	1		37	55	50	10	15		Drabek 1975
<i>Phoca vitulina</i>									
Weaned pup	1	0.56							J.M. Burns, unpublished data
<i>Pusa hispida</i> ^a	3	0.7							Crile and Quiring 1940
<i>Erignathus barbatus</i> ^a	1	0.5							Crile and Quiring 1940

Note: The heart form is expressed as height/circumference \times 100. The length and width of the right ventricle are indices of the length and width of the right ventricular chamber (see Drabek 1975). The maximal thickness of the nonseptal wall of the right ventricle is expressed as a percentage of the thickness of the wall of the left ventricle. The mass of the septal wall is included in the total heart mass and is not considered part of the right ventricle.
^aAge unknown.

Table 3. Comparisons of aortic bulb morphology.

Species	Aortic bulb		Source
	Increase (%)	Decrease (%)	
<i>Cystophora cristata</i>			
Weaned pups	44	—	This study
Yearlings	68	66	This study
Adults	67	—	This study
<i>Leptonychotes weddellii</i>	73	—	Drabek 1975
<i>Lobodon carcinophagus</i>	82	—	Drabek 1975
<i>Ommatophoca rossii</i>	53	—	Drabek 1975
<i>Hydrurga leptonyx</i>	33	—	Drabek 1975
<i>Neophoca cinerea</i>	—	50	King 1977
<i>Phocartos hookeri</i>	—	50	King 1977
<i>Mirounga leonina</i>	—	48	King 1977

Note: The percent increase in the aortic bulb is expressed as the inside diameter of the aortic bulb over the inside diameter of the base of the aorta. The percent decrease in the aortic bulb is expressed as the decrease in the outside diameter between the aortic bulb and the beginning of the descending aorta at the level of the ligamentum arteriosum.

using one-way ANOVA methods, and significance was assumed at $p < 0.05$.

Histology

Two tissue blocks (5×5 mm) were removed from the aorta of yearling female 2000.10 and yearling male 2000.11. One block was taken from the greatest diameter of the aortic bulb proximal to the brachiocephalic artery and the other from the descending aorta immediately distal to the ligamentum arteriosum. The blocks were embedded in paraffin, sectioned, and stained with Verhoeff's van Gieson for elastin by HistotechNologies, Inc., Cleona, Pa., following standard histological procedures (Presnell and Schreiber 1997). The sections were studied with light microscopy as follows: 10 randomly selected fields of the tunica media, in each of the two sections of the aorta, were studied at $\times 40$, with a $10 \times 10 \mu\text{m}^2$ disk in view. The number of elastin strands across one 10-square row were recorded in each of the 10 fields and averaged. The difference between the means of the number of elastin strands counted in the tunica media in the two aorta sections was compared.

Results

Heart morphology

The mass ($n = 23$) and shape ($n = 9$) of the hearts measured as part of this project are shown in Table 1. There were significant differences in the mass-specific heart mass of neonates, weaned pups, yearlings, or adult females on both a total (TBM) and lean (LBM) body mass basis (TBM: one-way ANOVA, $F_{[3,21]} = 5.72$, $p = 0.005$; LBM: $F_{[3,21]} = 3.51$, $p = 0.033$) (Table 2). In both cases, weaned pups had hearts that differed in relative size from those of adults (Tukey's HSD (honestly significant difference) test). However, the direction of difference varied. On a total body mass basis, weaned pups had hearts smaller than those of adults (0.59 vs. 0.68%), but when expressed on a LBM basis, weaned pups had hearts larger than those of adults (1.05 vs. 0.88%). There were no differences in relative heart size between adults and

yearlings or between neonatal and weaned pups (one-way ANOVA, $F_{[2,18]} = 3.18$, $p = 0.06$). Within age classes there was no difference between pup sexes (Student's t test, $p = 0.58$) or between the two collection years (Student's t test, $p = 0.09$ pups; $p = 0.11$ adults).

In appearance, the apex of the heart was rounded and was formed by the convergence of the right and left ventricles. Internally, the atrioventricular valves had the characteristic mammalian pattern of three cusps in the right valve and two cusps in the left valve, and the aortic and pulmonary valves each had the typical three semilunar cusps. Heart-form calculations indicate that the hooded seal's heart is short and broad, as is typical of other phocid seals (Table 2). However, the length and width indices of the right ventricular chambers show that the hooded seal has a longer right ventricle than other pinniped species for which such data have been reported (Drabek 1975; Bisaillon 1982). In addition, relative to the left ventricular wall, the right ventricular wall of the hooded seal is much thicker than in other species studied. Relative ventricular thickness declined with age: while the right ventricular wall was 84% as thick as the left in pups, it was only 58% as thick as the left in adults. This change likely reflects a greater increase in the myocardium of the left ventricle with age, rather than an atrophy of the right. This is confirmed by the fact that the right ventricle accounted for approximately 20% of the heart mass in all age classes, a slightly larger proportion than in other species.

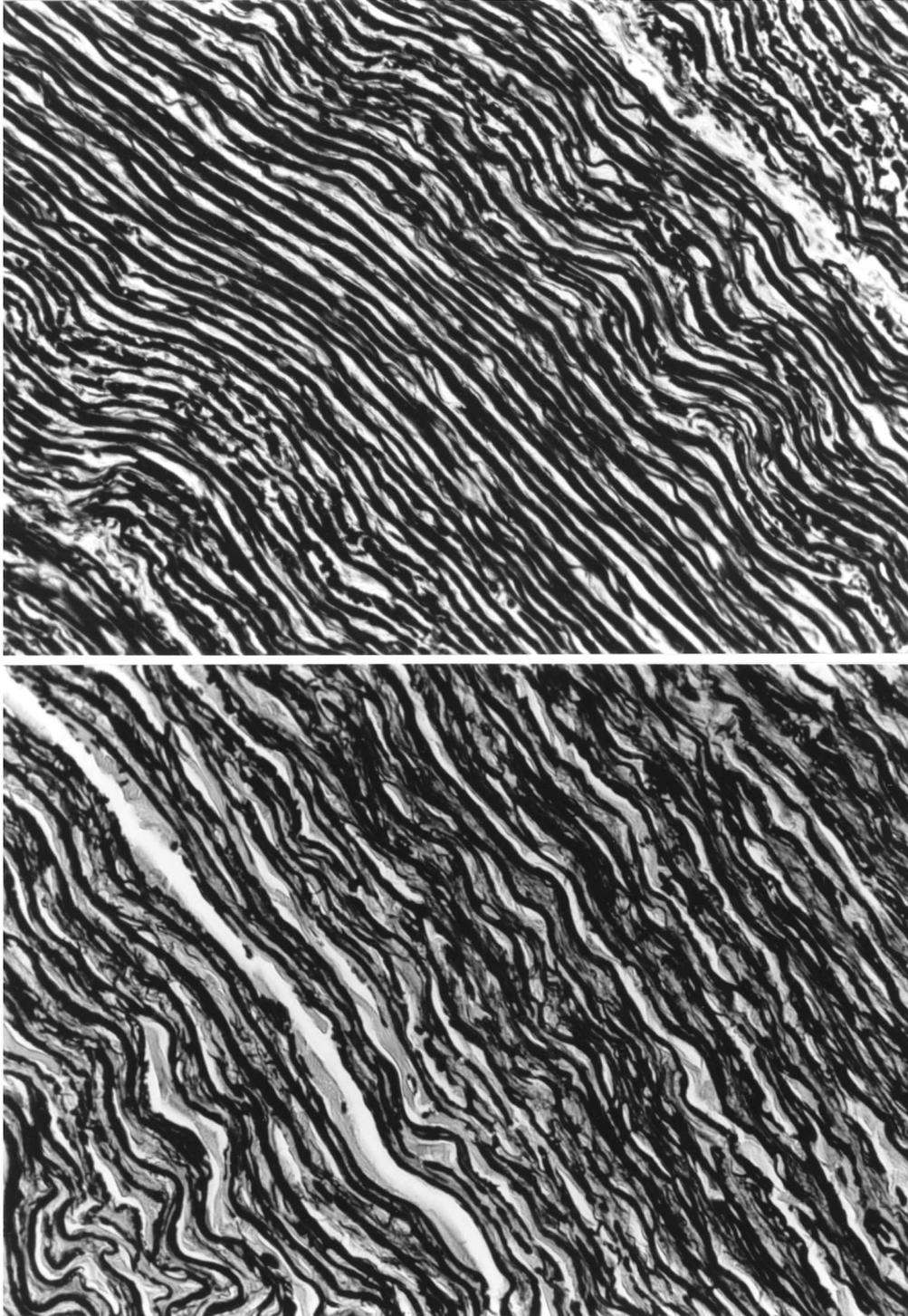
Aorta morphology and histology

The arch of the aorta had three main branches: a brachiocephalic artery, a left common carotid artery, and a left subclavian artery. The inside diameter of the aortic bulb increased 44% over the base of the aorta in the pups, and it increased 68 and 67% in diameter in yearlings and adults, respectively (Table 3). The descending aorta in the yearling hooded seal constricted markedly immediately following the aortic bulb at the level of the ligamentum arteriosum (Table 3). While the tunica media of the bulb consisted primarily of anastomotic elastin strands (Fig. 1), we found significantly fewer elastin strands in the tunica media at the level of the ligamentum arteriosum (yearling female 2000.10: bulb 32.1 ± 1.1 (mean \pm SE) fibers/area vs. 16.2 ± 0.9 fibers/area in the descending aorta). A similar pattern in the difference in elastin-strand density in the bulb and aorta was also seen in yearling male 2000.11 (bulb 23.9 ± 0.84 fibers/area vs. 15.3 ± 1.2 fibers/area in the descending aorta).

Discussion

Overall, the relative size of hooded seal hearts was similar to other phocids, which as a group have larger hearts than predicted on the basis of allometric scaling of mammalian heart size ($M_h = 0.0059 M_b^{0.98}$, where M_h is heart mass in kilograms and M_b is body mass in kilograms; Schmidt-Nielsen 1997). Using this equation, the average ratio of the observed heart mass to the expected heart mass in adult hooded seals is 1.2. The relatively large heart size of marine mammals has been related to their diving behavior (Ridgway and Johnston 1966; Bryden and Lim 1969). For example, Ridgway and Johnston (1966) hypothesized that the larger heart, higher hemoglobin concentration, greater blood volume, and larger

Fig. 1. Cross sections ($\times 400$) through the tunica media, showing a greater density of stained (Verhoff's van Gieson for elastin) elastin strands in the aortic bulb (top) than in the descending aorta immediately distal to the ligamentum arteriosum (bottom).



oxygen stores of Dall's porpoise (*Phocoenoides dalli*) were adaptations that permitted *P. dalli* to exploit swifter prey and feed at greater depths than *Tursiops truncatus*. However, in our study there was little evidence that heart size was correlated with diving strategy. Adult hooded seals had hearts that were similar in relative size to those of other phocids, despite the fact that they make remarkably long and deep

dives for their body size (Folkow and Blix 1995, 1999). And, while yearling hearts were proportionately larger than those of other species, this could be due to the small sample size.

From an anatomical perspective, the broad short heart of the adult hooded seal is similar to that of other adult phocids (Drabek 1975; Bisailon 1982). However, hooded seals do

have a longer right ventricle than reported for fissioned and other pinniped carnivores (Davis 1964; Drabek 1975), and the internal architecture of the right-ventricular chambers is most similar to that of the deep- and long-diving Weddell seal (*Leptonychotes weddellii*) (Drabek 1975). However, hooded seals of all ages had right ventricles larger and more robust than those reported for other seals (Drabek 1977; Bisaillon 1982). The proportionately large right ventricle might contribute to diving efficiency by permitting a greater cardiac output for a given pulmonary vascular resistance. This would increase lung perfusion during surface recovery. Therefore, if one interprets ventricular design as more reflective of physiological adaptations to diving than relative heart mass, then these data fit with the observed behavioral patterns.

Similarly, while the branching pattern of the greater vessels from the aorta in the hooded seal is like that reported for other phocids (King 1977), the size of the bulb in the ascending aorta (expressed as a percent increase in the aorta's greatest diameter, proximal to the brachiocephalic artery, over the diameter of the base of the aorta; Drabek 1975) is much greater than that reported for any seals other than the Weddell and crabeater seals (*Lobodon carcinophagus*). The descending aorta in the hooded seal constricts markedly immediately following the aortic bulb at the level of the ligamentum arteriosum. This, too, might represent an adaptation for deep and long dives. In 1888, Turner (quoted in King 1977) suggested that such a change in the diameter of the aorta of southern elephant seals would facilitate the blood flow in subsequent vessels. More recently, Hochachka (2000) used magnetic resonance imaging and magnetic resonance spectroscopy to image the heart, aortic bulb, and descending aorta of a juvenile northern elephant seal during a simulated dive. He found that the aortic bulb allowed continuous blood flow throughout both systole and diastole, and so removed the large changes in blood flow across the cardiac cycle that are typical of terrestrial mammals (Hochachka 2000). Thus, in hooded seals, the abrupt decrease in diameter, accompanied by less-elastic distensibility in the descending aorta immediately distal to the aortic bulb, likely helps maintain a high blood pressure during diving bradycardia. Overall, the morphological data suggest that hooded seals have a heart that is well suited to long and deep diving.

It was also possible to assess the ontogenetic changes in heart morphology and compare them with earlier work done by Bryden and Lim (1969). These authors found that the hearts of newborn southern elephant seals were relatively large at birth, decreased in *relative* mass during lactation, and then increased again during the post-natal fast. They considered this last change to be representative of growth of the heart at the beginning of the weaned pup's diving activity and to be indicative of the developing diving and breath-holding ability. However, our findings suggest that instead of differential rates of heart growth, changes in relative heart mass are due to age-related changes in body composition. At the end of the lactation period, weaned hooded seal pups were 44% fat, approximately 20% more than all other age classes. Thus, it is not surprising that they had the smallest heart size, when size was expressed *on a total body mass basis*. However, when their heart size was expressed on a lean body mass basis, they had hearts that were 20% larger than

adults. In combination, these findings suggest that age-related changes in organ sizes must account for the rapid accumulation of blubber during the nursing period, and the subsequent reduction in fat mass during the post-weaning fast.

While the interplay between body composition, body mass, and heart mass is one reason that there was little change in the relative heart mass of hooded seals with age, it is possible that this was due instead to the maturity of the pups at birth and their rapid growth rates during lactation. Hooded seal pups are large at birth (12% of the maternal mass) and are one of only two phocid species born with adult pelage and a subcutaneous blubber layer (Ofteidal et al. 1991). The precocial status, short lactation period (4 d), and fast growth rates (up to 7 kg/d) of the pups is thought to be related to the unstable sea ice substrate on which they are born (Bowen et al. 1985), but the chance of early entry into the water may also have selected for early development of the cardiovascular system. Indeed, the heart is a much larger fraction of the total muscle mass of pups than it is of adults (3.45 vs. 2.42%, muscle mass determined by complete dissection; J.M. Burns, unpublished data). In addition to being large, the heart appears to be relatively mature: unlike other species (Castellini et al. 1994; Zenteno-Savin 1997), young hooded seal pups demonstrate bouts of sleep apnea, and these bouts are accompanied by marked bradycardia (J.M. Burns, unpublished data).

In summary, the hooded seal is unique in being a small-sized seal capable of long deep dives. The morphology of the heart and ascending aorta of the hooded seal is probably related to its diving behavior. The relatively large heart, the large right ventricle, and the prominent aortic bulb in the pup, probably reflect the pup's rapid growth and efficient development. Such morphological features likely play an important role in the development of diving behavior. A large right ventricle would increase lung perfusion during surface recovery, and the aortic bulb would be important in maintaining high arterial pressure and continuous blood flow throughout both systole and diastole during diving bradycardia. All such adaptations would contribute to foraging efficiency.

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